

anterior palatine foramina 6.5×2.7 ; length of upper molar series 5.7.

Hab. Jampea Island, Saleyer group.

Coll. A. H. Everett, Dec. 1895.

A second specimen (female) has its head and body 125 millim., tail 169, hind foot 29.5, and ear 18.

This species seems to be most closely allied to *Mus Becarii*, Jent., from which it differs by its rather larger size or, at least, longer hind feet, the absence of any terminal pencilling to the tail, its grey-mixed belly, white feet, the normal projection forward of the zygoma-root, and the further extension backward of the anterior palatine foramina.

XXXIX.—The Pholadidæ.—II. *Note on the Organization of the Larva, and the Post-larval Development of Ship-worms.*

By C. P. SIGERFOOS*.

A YEAR ago I published† a note on the early stages of development of the Pholadidæ, in which the breeding-habits of *Pholas* and three species of ship-worms were described. During June and July of 1895 I again visited Beaufort, N. C., with the Johns Hopkins Marine Laboratory, and collected all stages of one of these species (*Xylotrya fimbriata*) from the small bivalve that has just become attached to the adult. As the eggs of this species are extruded freely into the water, I have not been able to observe the stages between the oldest larvæ raised in aquaria from artificially fertilized eggs and the attached stage, in which the development is much more advanced. For these intermediate stages it is necessary to resort to species which retain the embryos in the gills.

The free-swimming stage is reached in three hours, and in a day a well-developed shell has been formed. The young of Lamellibranchs develop but slowly, and though we have no direct observations as to the time the ship-worm larva is free-swimming, we may assume, I think, that it is at least a month, it may be two. During this time most of its energies are expended in locomotion, while after it has become attached it may devote all of its energies to forming its burrow and to securing food for itself; so that its rate of growth is very rapid. The larvæ become attached very

* From the 'Johns Hopkins University Circulars' for June 1896, pp. 87-89.

† 'Johns Hopkins University Circulars,' no. 119, June 1895; Ann. & Mag. Nat. Hist. [6] xvi. p. 233 (1895).

freely to boxes hung in the water, and in this way I was able to secure all stages of development and to observe the rate of growth. I have observed as many as thirty to 1 square centim. of surface. Coming in contact with the wood, the larva throws out a single long byssus-thread for attachment, and never again leaves its place. The velum is lost within a few hours, and the transformation of the small bivalve into the ship-worm is begun. The newly attached larva is somewhat less than 2.5 millim. long. In 12 days it has attained a length of 3 millim.; 16 days, 6 millim.; 20 days, 11 millim.; 30 days, 63 millim.; and 36 days, about 100 millim., when it bears ripe eggs or sperm. In four to five weeks small timbers may be completely ruined in the warm water at Beaufort.

Organization of the Larva.

In striking contrast with the adult, the larva (shown in longitudinal vertical section in fig. 1) is perhaps more foreshortened than that of any other Lamellibranch. The valves of the shell are elliptical in outline, somewhat wider than long. Seen dorsally they are circular in outline. The left valve bears two teeth, the right three. The long internal process of later stages (apophysis) is present as a rudiment.

The velum still occupies a large space (*VC*) in the anterior dorsal region. I have never seen it extended after the larva had become attached. Both siphons (*A* and *R*) are already formed, and from their point of union the septum has grown forwards and become attached to the foot. The gills of this stage have developed but little beyond the last stage figured by Hatschek. There are on either side two gill-slits, with a rudiment of a third. The "filaments" are true gill-bars, for they are attached to the foot by their ventral end.

The foot is present as a very long tongue-shaped structure, with a byssus apparatus at its posterior ventral angle. In fig. 1 the foot is shown considerably contracted, occupied mostly by mucus-cells and the byssus apparatus.

The retractors of the foot are attached to the umbonal region of the valves. Both adductor muscles are present, the posterior already the larger of the two (*Aa* and *Ap*).

The nervous system is already highly developed (figs. 1 and 2). All of the ganglia are well formed, and the commissures form well-defined nerves. *The cerebral and pleural ganglia are still separated by a short commissure.* The pleural (*Pl*) is lateral to the cerebral (*C*), and from its posterior angle the pleuro-visceral commissure passes. The pedals

Fig. 1.

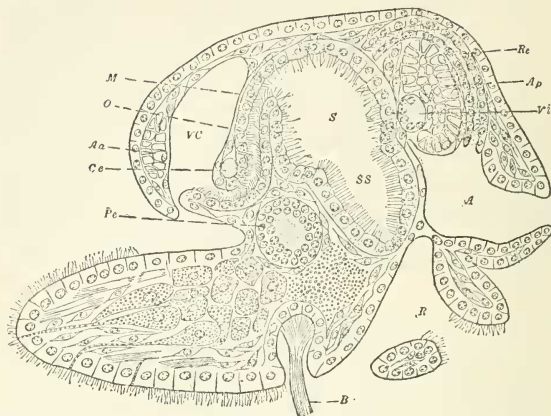


Fig. 2.

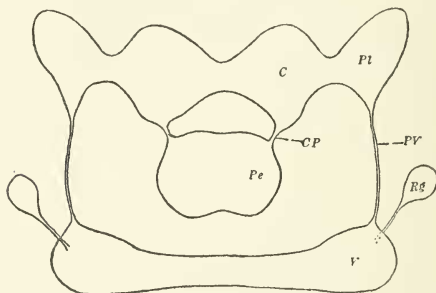


Fig. 1.—Longitudinal vertical section of newly attached ship-worm.
The disintegrated cells of the velum are not shown.

Fig. 2.—Outlines of the ganglia of nervous system, dorsal view. Only commissural nerves are shown.

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| A. Anal siphon. | Pe. Pedal ganglion. |
| Aa. Anterior adductor muscle. | Pl. Pleural ganglion. |
| Ap. Posterior adductor muscle. | R. Respiratory siphon. |
| B. Byssus thread. | Rg. Ganglion of respiratory nerve. |
| C. Cerebral ganglion. | S. Stomach. |
| Ce. Cerebral commissure. | SS. Sheath of crystalline style. |
| CP. Cerebro-pedal commissure. | V. Visceral ganglion. |
| M. Basement-membrane of velum. | Vi. Visceral commissure. |
| O. Æsophagus. | VC. Velar cavity. |

(*Pe*) are as much concentrated as they will become. The otoliths lie lateral to their posterior edges and persist to the adult condition. The visceral ganglia (*V*) are still wide apart and lie in front of the posterior adductor muscle (*Vi*). With their commissure they form a cylindrical mass four or five times as long as its diameter and somewhat enlarged at the two ends, the ganglia proper. The ganglion of the respiratory nerve (*Rg*) is still wide apart from the visceral.

The alimentary canal is already highly specialized. A rather long œsophagus (*O*) leads into the stomach (*S*), on either side of which a single liver-lobule is borne. From the *posterior* part of the stomach the sheath of the crystalline style (*SS*) has grown, and, though small, its wall is already composed of large, clear, slightly granular cells, bearing long dense cilia. The intestine leaves the right side of the stomach in front, forms a single loop, and bends upwards and backwards to hang over the posterior adductor (*Re*). From the middle of the right side of the stomach the cæcum has grown as a small hemispherical bag, though it is still functionless.

The renal organs are present and lie ventral to and in front of the posterior adductor muscle. Near the cerebral ganglion on either side is a glandular structure which I shall describe later.

Metamorphosis and Adult Structure.

Once attached, the larva probably never leaves its place. The velum is very soon lost, and has an interesting fate. The long lower lip is thrown forward to the mantle in front under the velar cavity, so that the cells of the velum which are *cast off* have but one mode of escape, into the œsophagus. *They break off* from the basement membrane and *are eaten*. Within a few hours the membrane contracts so as to wholly obliterate the velar cavity. This fate of the velum is interesting, for it has been described as entering into the formation of the labial palps. But in this species there are no palps, and it would not do to generalize to other forms. However, in the oyster, where the palps become very large, they are very small at first, much smaller than the velum, though they are not developed till after the oyster has become attached.

The foot very soon (within a day) becomes the pestle-shaped cupping organ, which assists the shell in boring. The byssus apparatus is functional for a day or two, and then degenerates, though it persists in the posterior part of the foot as a small closed vesicle, as in *Cyclas*.

The burrow is formed as follows:—Almost as soon as the larva has settled it begins to clear away a place by means of the ventral edges of the valves of the shell. In this way a small pit is formed. But very soon rows of teeth are formed in succession on the anterior edges of the valves; the small knobs are formed on their umbonal and ventral regions; the ligament becomes functionless, and the two adductors become antagonistic to each other. The teeth are formed independently, and afterwards are cemented to the valves, pointing outward and backward. While the foot performs a cupping action, the posterior adductor contracts, the two valves swing on each other by means of the two pivots formed by the knobs, and the teeth are brought to bear on the wood, rasping away its surface.

The essential changes in the nervous system are the fusion of cerebral and pleural ganglia and the concentration of the viscerals and their shifting in position. The cerebrals and pleurals have fused in specimens 5 millim. long, but their double origin is still indicated. The visceral ganglia become concentrated in specimens 1 millim. long, and shift from a position anterior to the posterior adductor to one ventral to it, and at last come to lie far behind it in the adult. It seems interesting that the description of the nervous system given by Quatrefages * is still accepted, except with slight modifications in the viscerals as given by Pelseneer. Quatrefages described the cerebral ganglia as fused, the pedals as rudimentary and separate. On this ground, with others, he proposed to separate the Terevidæ from the Pholadidæ. He mistook the pedal for the cerebral, but I am unable to say what he described as the pedal. The pedals are fused from the first and never become rudimentary, though their development is not nearly so great as that of the visceral. The cerebro-pleurals remain separated by a *long* commissure and lie almost at the sides of the mouth.

The gills of the ship-worms are more specialized and more interesting than has heretofore been supposed. Beginning with the two "filaments" present in the larva, new filaments are added posteriorly by the appearance of slits in the gill-fold. These filaments are in reality bars, for the slits are perforations which do not penetrate to the ventral border of the fold. The fold progressively fuses with the body at its ventral border. In this way a series of bars is formed attached at both ends. This mode of formation persists through life, except that after the tenth (usually) a second

* 'Annales des Sciences Naturelles,' Zool. sér. 3, t. xi.

slit appears ventral to the first, so that each filament is separated from its fellows by double slits. That last formed corresponds to the space between the ascending limbs of adjacent filaments. The first ten filaments, then, have no ascending limbs. Deshayes described * a series of plications in the anterior part of the body, and thought them to be normal structures. These are the first ten filaments formed, which have later become separated from their fellows posteriorly by a great distance, as follows:—When the young *Teredo* is somewhat less than 1 centim. long each gill consists of a long series of about seventy-five filaments, stretching uniformly from the anterior part of the body to the small filaments which have just been formed. But now the ninth or tenth filament broadens (grows in line of the antero-posterior axis of the animal) till in large specimens of the adult the anterior filaments may be separated from the posterior part of the gill by 10 centim. or more. The ciliated furrow described by Deshayes connects the two portions. The epibranchial cavity persists as a long canal between the two parts. Fusions between adjacent filaments of the first ten take place, so as to more or less obliterate the gill-slits.

Contrary to the statement of Quatrefages, there is a single gill (a half ctenidium in modern usage) on either side. This is the internal gill, and the external has wholly disappeared.

Closely associated with the gill is a very prominent glandular structure peculiar to the ship-worms. Deshayes described a special gland in the umbonal region, and surmised its function to the formation of a secretion for softening wood by chemical action. Grobben † did not find it, and questioned its existence. Deshayes also described mucus-glands in the gills, whose secretion he supposed to be for the nutrition of the embryos in these viviparous forms. Both are parts of the same organ. In the newly attached larva there is a considerable glandular structure on either side in the anterior part of the body, whose duct opens under the cerebral ganglion in front of the mouth. As the animal grows the gland grows posteriorly, sending branches into the gill-filaments. As the two parts of the gill become separated, the two parts of the gland remain connected by a long narrow (?functionless) duct, which accompanies the epibranchial canal. Further than this I am at present unable to describe this organ, which is very difficult to study. Since in this species, which does not retain its embryos, the posterior part is present in young

* 'Histoire naturelle des Mollusques.'

† Arbeiten Zool. Inst. Wien, Bd. vii. (1886).

and old and in males and females, its function cannot be the formation of a secretion to nourish the embryos.

The posterior part of the body, usually called the muscular collar, is a very interesting region, containing a complex of several well-defined muscles. The collar is attached to the calcareous tube in an irregularly elliptical line. The outermost part is the line of origin of the *protractor of the pallet*, which radiates from the inner end of the handle of the pallet, its insertion, to its line of attachment. To the inner line is attached the *retractor of the siphons*, which is almost wholly distributed to the respiratory siphon. A well-defined muscle, the *adductor of the pallets*, connects the upper parts of the handles of the pallets. From the upper end of the handle a small muscle, the *retractor of the pallet*, passes to the body forwards. The animal defends itself as follows:—While the siphons are retracted the pallets are protracted to completely close the tube at its outer end. The siphons are extended by an inflow of blood, and the pallets are retracted by the action of their retractors, accompanied by the adductor of the pallets.

In specimens 3 millim. long, in which the visceral ganglia have taken up the position of the adult, the sexual organ is present on either side as a rudiment of a small mass of cells ventral to the ganglia. From this part branches grow out, and the lumen appears later. That in the oldest part of the gland becomes the main part of the genital duct. In addition, there is in the genital papilla a small ectodermal invagination, which much later unites with the part which is of mesodermal origin. The part which is of mesodermal origin forms sexual cells, at least at first. The sexes are separate from the first. Protandry is not present. Only rarely are individuals hermaphrodite.

The ship-worm larva is already highly organized when it becomes attached. A functional byssus apparatus is present. The cells of the velum are cast off and eaten. The cerebral and pleural ganglia are still separate. The crystalline style arises from the posterior part of the stomach. While the foot performs a cupping action to draw the shell close against the surface of the wood, the contraction of the posterior adductor muscle causes the two valves to swing upon each other, and the teeth rasp away the wood.

Contrary to the description of Quatrefages, the pedal ganglia are not separate and not rudimentary; the cerebrals are not fused, but separated by a long commissure. The first-formed filaments of the adult gill have no ascending limbs. They form a series of bars in the anterior region of

